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Original article

Seed dispersal and spatial distribution of *Attalea geraensis* (Arecaceae) in two remnants of Cerrado in Southeastern Brazil

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ABSTRACT

The seed dispersal system of *Attalea geraensis* (Arecaceae), an acaulescent palm, was investigated during one year in two Cerrado fragments in the state of São Paulo, southeastern Brazil. *A. geraensis* had inflorescences and infrutescences throughout the year. Two scatter-hoarding rodents (the spiny rat, *Clyomys bishopi* and agoutis, *Dasyprocta azarae*) were identified as seed predators/dispersers, able to move seeds up to 30 m from the palms, although most of the fruits (57.5%) were dispersed less than 2 m. The removal rates were high and after 20 days, 97.2% of the fruits were removed. Fruit fate was not related to fruit mass, length and diameter. The application of Morisita's index showed a more clumped distribution of adults in the smaller fragment, probably because of the absence of agoutis. Higher seed removal by rodents in the large Cerrado remnant may decrease seed predation by beetles.

1. Introduction

Seed dispersal is a central demographic process to plant populations (Harper, 1977; Jordano, 2000; Levine and Murrell, 2003). Seed dispersal curve can set if seedlings will be more or less aggregated and whether they will reach or not favourable patches (Janzen, 1970; Barot et al., 1999a). Therefore, seed dispersal is related to demographic parameters, such as seed or seedling survival (Barot et al., 1999b). In tropical regions, animals are the main seed dispersers of most plants and their foraging behavior may have strong effects on plant distribution (Jordano, 2000). In Cerrado, a savanna-like vegetation, the most common dispersal mode is zoochory, which can involve up to 68% of all woody species (Gottsberger and Silberbauer-Gottsberger, 1983; Vieira et al., 2002). One of the most common plant families in the Cerrado, in terms of individuals, is the Arecaceae. The seed dispersal system of the Arecaceae is chiefly zoochoric (Zona and Henderson, 1989), with the seeds representing a very important component of the diets of mammals, especially in periods of fruit scarcity (Terborgh, 1986; Peres, 2000; Silvius, 2002). The importance of palms may be even higher in highly seasonal ecosystems, such as savannas. In the Cerrado, peak fruit production has been recorded between November and February, the most

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humid months of the year, when fruits can remain attractive for a longer time (Batalha and Mantovani, 2000).

The genus *Attalea* contains at least 29 species that occur in the Neotropics, in tropical forests and savanna-like vegetation that corresponds to Cerrado (Henderson et al., 1995; but see Lorenzi et al., 2004). Twenty of these species are found in Brazil (Henderson et al., 1995), but studies related to seed dispersal in this genus have dealt with only six species. These studies have shown that most species of *Attalea* are dispersed by mammals, some of them exclusively by scatter-hoarding rodents (Forget et al., 1994; Peres, 1994; Kays, 1999; Fragoso and Huffman, 2000; Wright et al., 2000; Wright and Duber, 2001; Vieira, 2002; Fragoso et al., 2003; Pimentel and Tabarelli, 2004).

The fruits of *Attalea geraensis*, which have a smooth mesocarp that is appreciated by rodents (Lorenzi et al., 1996, 2004), are commonly found in galleries of the spiny rat *Clyomys bishopi* (Vieira, 2002). The hard dry fruit is apparently not attractive to other frugivores of the Cerrado except for peccaries, which are seed predators (Neri, 2004).

Palms are considered to be a very important resource to the vertebrate fauna, as there are many species which produce fruits during the period of fruit scarcity (Terborgh, 1986). Therefore, the aim of this work was to study the interaction between the frugivorous mammal fauna and *A. geraensis* in Cerrado vegetation. We were particularly interested in (i) determining the availability of *A. geraensis* fruits throughout the year, (ii) verifying the influence of fruit mass, length and diameter on the number of seeds and on the distances that fruits were removed by mammals from parent plants, (iii) comparing the spatial distribution of *A. geraensis* adult palms, and (iv) the proportion of seeds preyed upon by insects and mammals in two fragments of Cerrado with different degrees of defaunation.

2. Material and methods

2.1. *Study sites*

This study was done at two sites located in the central part of São Paulo state, southeastern Brazil, where the predominant vegetation is Cerrado (Fig. 1). The largest fragment (about 9010 ha) was the Estação Ecológica de Jataí (hereafter referred to as the ''large fragment''), which was located in the municipality of Luiz Antônio (21°33′S, 47°45′W). This site has a wide variety of habitats, from aquatic (rivers and lagoons) to vegetation completely free of inundation, such as cerrado *sensu lato* (which accounts for most of the area) and parts of semideciduous forest (Santos et al., 2000). The climate is Aw, according to the Köppen classification, and is characterized by two distinct seasons: one humid, with high temperatures and abundant rainfall (from November to April) and the other dry, which has lower temperatures and less frequent rainfall (from May to October). The frugivorous mammal fauna of this fragment consists of manned wolves (*Chrysocyon brachyurus*), crab-eating foxes (*Cerdocyon thous*), collared peccaries (*Tayassu tajacu*), agoutis (*Dasyprocta azarae*) and spiny rats (*Clyomys bishopi*; Talamoni, 1996).

The second study site is a 528 ha Cerrado reserve on the *campus* of the Universidade Federal de São Carlos (hereafter referred to as the ''small fragment''), located in São Carlos (21°58′S and 47°52′W), about 90 km from the large fragment. About 124.7 ha of this site corresponds to Cerrado *sensu lato*, 3.6 ha to gallery forests, 93.8 ha to *Eucalyptus* forest and 83.7 ha to ponds, trails and modified fields (Santos et al., 1999). The climate is Cwa (tropical of altitude) – warm with a dry winter, in which the average temperature of the coldest month is $<18°$ C and of the hottest is $>22°$ C. Rainfall in the driest month is <30 mm, but is ≥ 10 times higher in the moistest month. This site is characterized by habitat fragmentation and anthropogenic interference (Motta-Junior et al., 1996) and lacks large ungulates and large carnivores. Although endangered species of frugivores, such as the manned wolf (*C. brachyurus*) occur at this site, their abundance in this area is very low, as is that of agoutis (*D. azarae*) and collared peccaries (*T. tajacu*; Motta-Junior et al., 1996).

2.2. *Study species*

A. geraensis Barb. Rodr. is a monoecious acaulescent palm, rarely more than 1 m tall that occurs in Cerrado or dry forests of the Brazilian states of São Paulo, Minas Gerais, Rio de Janeiro, Goiás and Bahia, and also in Paraguay (Henderson et al., 1995). *A. geraensis* has 2–11 leaves with leaflets regularly arranged in the same plane and brown scales on the lower surface. The palms start to bear fruit when 3–5 years old (Lorenzi et al., 1996, 2004). *A. geraensis* endocarps can have from 1 to 3 seeds (Fig. 2).

Many species of *Attalea* can thrive in disturbed areas, such as cleared pastures (Henderson et al., 1995; Lorenzi et al., 1996, 2004; Souza et al., 2000), and in areas with intense use of fire. Indeed, when fires are not very frequent, *Attalea* species show increased fecundity, growth under open canopies and larger nutrient availability after burning (see Souza and Martins, 2004, for *Attalea humilis*).

2.3. *Phenology*

We conducted a phenological study in both study areas from April 2003 to March 2004. In each fragment, we monitored 12 adult palms in the first week of each month. The characteristics recorded every month included the number of leaves, inflorescences, infrutescences and fruits per infrutescence. The Mann–Whitney *U*-test was used to compare the number of inflorescences, infrutescences and fruits at both sites, whereas the number of leaves was compared using Student's *t*-test for independence. Student's *t*-tests and regression analysis were performed for the variables which were normally distributed. These analyses were done using the software JMP, version 5.0.1 (SAS Institute, 2002).

2.4. *Morphological description of* A. geraensis *fruits*

To determine the number of seeds per fruit, we collected 62 mature fruits from six palms from the large fragment in October 2003. We opened the fruits with a hammer and the number of seeds was recorded. Linear regression tests were used to determine whether fruit mass, length and diameter were related to the number of seeds.

2.5. *Endocarp census*

We did an endocarp census at both study sites in November 2003 in order to assess the relationship between endocarp

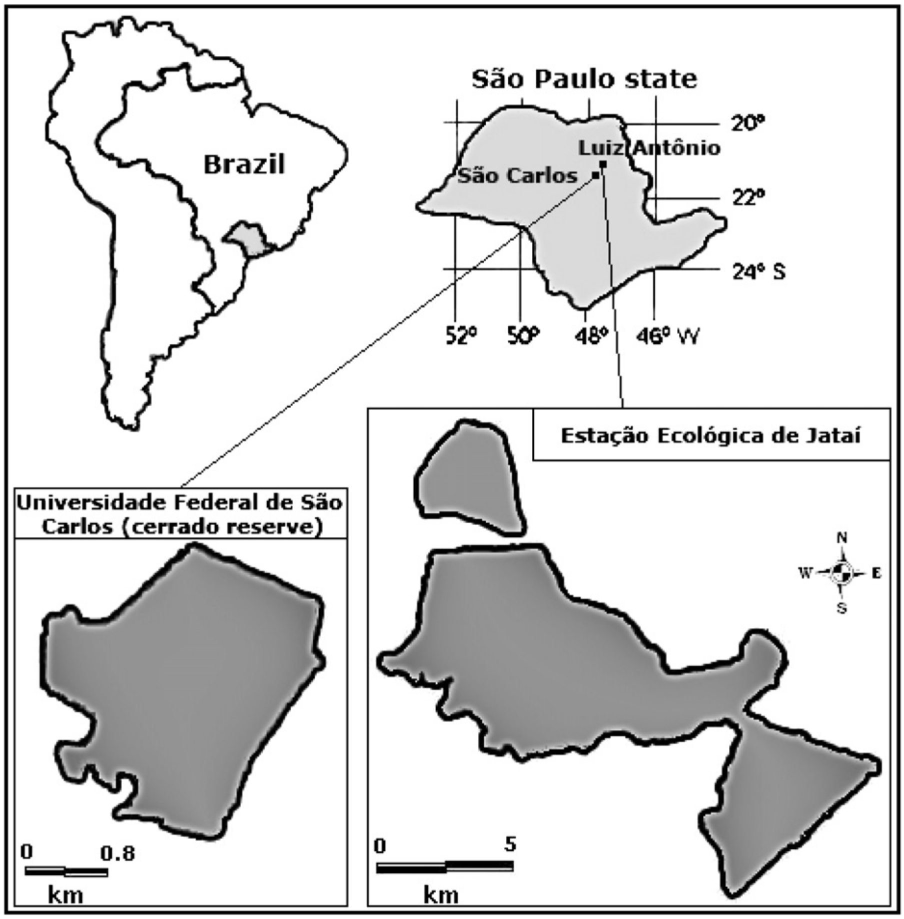

Fig. 1 – Location of both study areas in southeastern Brazil. The small fragment is located at the Universidade Federal de São Carlos (528 ha) and the large fragment is the Estação Ecológica de Jataí (9,010 ha).

density and seed mortality caused by insects and mammals (Galetti et al., 2006). In each fragment, we randomly chose 21 palms located along three trails. The endocarps on the ground surface and those buried superficially (less than 2 cm deep) within a 2 m radius of the palms were counted (Cintra, 1997; Wright and Duber, 2001) and classified as (i) preyed upon by insects, (ii) preyed upon by mammals or (iii) intact. Endocarps with symmetrical holes approximately 0.5 cm in diameter and with holes with characteristic rodent teeth marks in the central part were considered to be in the first and second categories, respectively (Forget et al., 1994; Wright et al., 2000). The chi-square test was used to compare the frequency of predation on endocarps by insects and mammals between the fragments.

2.6. Spatial distribution

To determine the spatial distribution of *A. geraensis* adult populations, we randomly placed 12 plots of 5 m × 10 m along three trails of the large and small fragments in August 2004. The distance from the plots to the trails varied randomly from 0 to 50 m. In the large fragment, the size of the area sampled was 37 ha while in the small fragment it was 2 ha. We used a standardized Morisita's Index of Dispersion (Morisita, 1962; Smith-Gill, 1975) to evaluate the distribution pattern of *A. geraensis* adults in the large and small fragments. This index ranges from −1.0 to +1.0, with 95% confidence limits at +0.5 and −0.5. Random patterns give an $I_P = 0$, clumped patterns, an $I_P > 0$ and uniform patterns, an $I_P < 0$ (Krebs, 1998). We also compared the spatial distribution between the fragments using the Mann–Whitney *U*-test.

2.7. Fruit removal experiment

We did a fruit removal experiment in the large fragment to estimate the dispersal distances and fruit fate (Cintra, 1997; Donatti, 2004). Mass, length and diameter of the fruits used in the experiment were measured to detect whether there was selection of fruits with different morphological characteristics (Brewer, 2001). Linear regression tests were used to answer to the following question: Is the removal distance of the fruits used in the experiment influenced by fruit mass, length and diameter?

Fruit fate was classified according to Forget (1996) and Silva and Tabarelli (2001) as: (i) not removed, (ii) preyed upon by mammals, (iii) dispersed with pulp consumed, (iv) dispersed and scatter-hoarded, (v) dispersed more than 30 m and (vi) lost. Classes (iii), (iv) and (v) were combined for the present

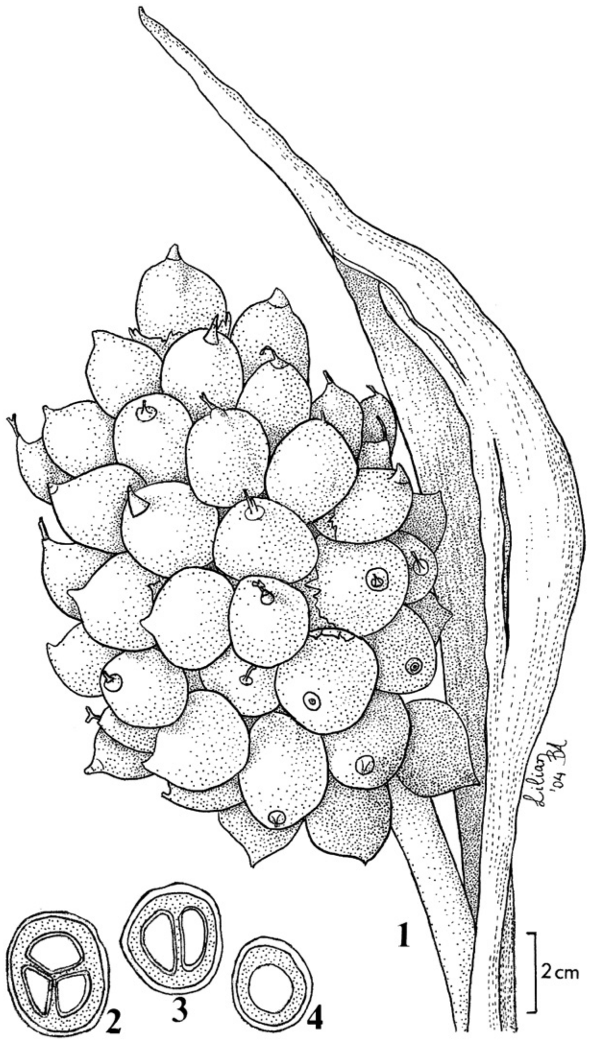

Fig. 2 – Infrutescence of *A. geraensis* Barb. Rodr (1) and cross-sections of fruits with three seeds (2), two seeds (3) and one seed (4).

study. Logistic regression analysis was used to test whether there was a relationship between fruit fate (hoarded and not hoarded) and fruit traits (mass, diameter and length).

We arranged 144 mature fruits under 36 parent plants (4 fruits/plant) located along four trails. Fine backstitch thread was attached to a 5 mm metal ring that was passed through a 2 mm hole in each fruit to allow the retrieval of removed fruits (Forget, 1996; Donatti, 2004). This metal ring was used to make it more difficult for the frugivore to gnaw through the line and carry the fruits away. The spool was placed inside a film pot around a 6 cm screw so that it would be easier to spool. The film pot was tied to the leaf scale. Each spool had 30 m of thread. The test was prepared on October 26th, 2003 and the results were recorded after 10 and 20 days (5th and 15th of November, 2003), the period that represents the season of abundant fruit (Gottsberger and Silberbauer-Gottsberger, 1983; Batalha and Mantovani, 2000).

3. Results

3.1. *Phenology*

There were no significant differences in the number of inflorescences, infrutescences and fruits between fragments. However, the number of leaves was significantly higher in the large fragment compared to the small fragment (Table 1).

A. geraensis showed inflorescences and infrutescences throughout the 12-month study. Although fruits were produced every month, from September 2003 to February 2004, there was a decline in the number of infrutescences at both sites (Fig. 3A-C). We recorded the presence of ripe fruits (fruits were considered to be ripe when they easily came unfastened from the infrutescence and also exhaled a characteristic sweet odor) in the dry and wet seasons, but found few ripe fruits among the palms studied; only 5.6% and 6.7% of the infrutescences had ripe fruits in the large and small fragments, respectively. The time-lapse from inflorescence to fruit ripening was 9 months (based on data for just one palm).

3.2. *Morphological description of fruits*

A. geraensis fruits have 1–3 seeds, with one-seeded fruits being the most frequent and three-seeded fruits the least frequent; 51.6%, 38.7% and 9.7% of the fruits had one, two and three seeds, respectively. The mean (±SD) of seeds per fruit and the median were 1.58 ± 0.67 and 1, respectively ($N = 62$). The number of seeds increased linearly with increasing fruit mass and diameter, but was not related to fruit length, as shown by linear

Table 1 – The mean number of leaves, inflorescences, infrutescences and fruits for *Attalea geraensis* in two Cerrado remnants in southeastern Brazil

Fragment	Leaves	Inflorescences	Infrutescences	Fruits
Small	5.1 ± 1.8	0.08 ± 0.34	0.94 ± 0.90	11.18 ± 10.4
Large	6 ± 1.9	0.14 ± 0.37	0.75 ± 0.84	15.10 ± 11.4
Mann–Whitney *U*-test *z*(*U*)	–	0.63 ns	0.79 ns	1.67 ns
t-test	3.93*	–	–	–

*$P < 0.001$, ns = not significant.
The numbers were determined from April 2003 to March 2004 and are expressed as the mean ± SD per individual of *A. geraensis*. The Mann–Whitney *U*-test was used for the number of inflorescences, infrutescences and fruits, and Student's *t*-test for the number of leaves in large and small fragments.

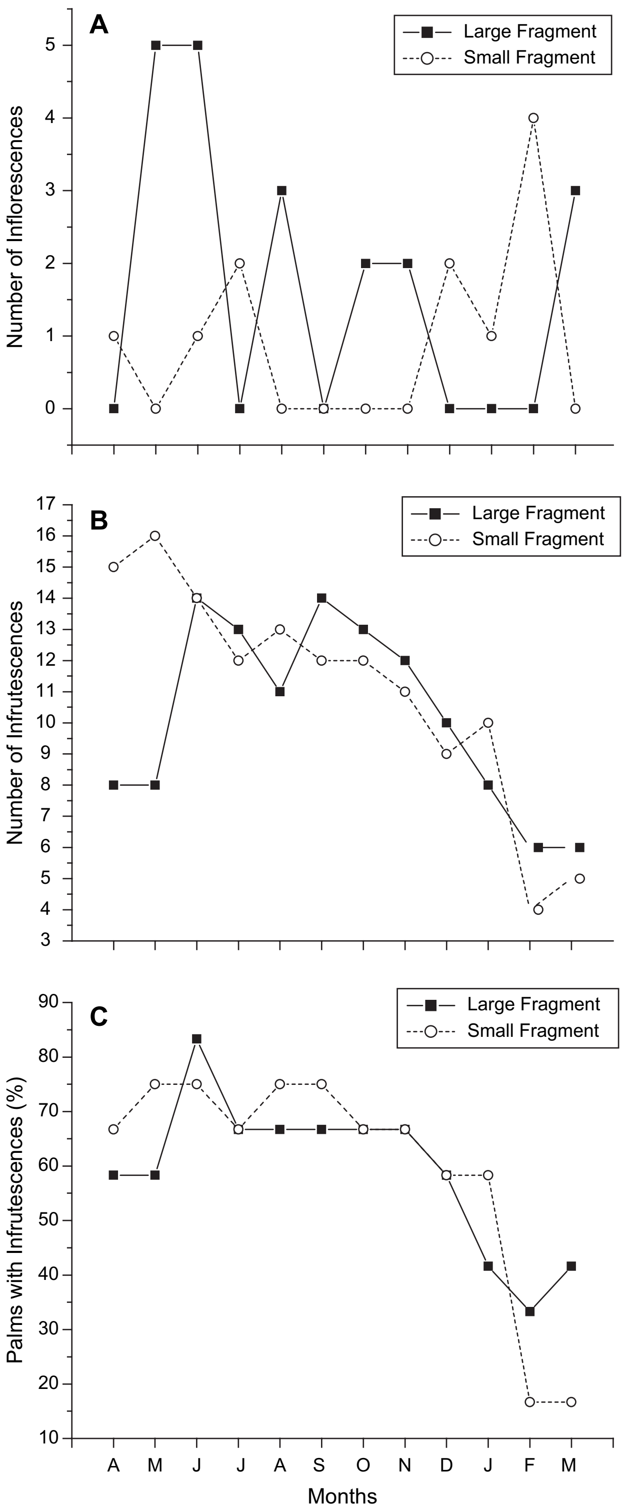

Fig. 3 – Phenological records for *A. geraensis* from April 2003 to March 2004 in the large and small fragments. (A) Number of inflorescences per month. (B) Number of infrutescences per month. (C) Percentage of palms bearing fruits.

regression analysis ($R^2_{mass} = 0.30$, $P < 0.0001$; $R^2_{diameter} = 0.23$, $P = 0.023$; $R^2_{length} = 0.009$, $P > 0.05$, $N = 62$). Mean fruit length, diameter and mass were 44.26 mm (±5.96), 27.08 mm (±4.3) and 19.87 g (±6.73), respectively, ($N = 206$).

3.3. *Endocarp census*

We collected 360 endocarps, with 273 being from the small fragment and 87 from the large one. The frequency of seeds preyed upon by insects and rodents varied significantly between fragments ($\chi^2 = 55.6$, $P < 0.001$). Both the large and small fragments had more seeds preyed upon by insects. However, there were more seeds preyed upon by rodents in the large (31%) than in the small fragment (5.1%), while insect predation follow the opposite pattern, where the large fragment had a smaller number of seeds preyed upon by insects (34.5%) than the small fragment (73.6%) (Fig. 4).

3.4. *Spatial distribution*

The large fragment had a lower density of adult palms (1.25 ± 2.2 palms per 50 m^2 plot, or, 250 ± 435.9 palms ha^{-1}) than the small fragment (2.4 ± 6.8 palms per 50 m^2 plot or 483.3 ± 1365.7 palms ha^{-1}). The small fragment had a more clumped distribution ($I_P = 0.81$) than the large fragment ($I_P = 0.51$). There was a significant difference in the density of *A. geraensis* between the two fragments ($U = 73.6$, $P < 0.05$).

3.5. *Fruit removal experiment*

After 20 days, 97.2% of the fruits used in the experiment ($N = 144$) had been removed. Of 144 fruits, 95 (65.9%) were scatter-hoarded, 38 (26.4%) were lost, four (2.8%) had the pulp gnawed, two (1.4%) were dispersed more than 30 m from the parent plant, one (0.7%) had the seed predated and four (2.8%) were not removed (Fig. 5). Most of the removed fruits (87 out of 140) were carried less than 2 m away from the parent palms (Fig. 6).

The linear regression test showed that the dispersal distances were unrelated to fruit mass, length and diameter ($R^2_{mass} = 0.000883$, $P > 0.05$; $R^2_{length} = 0.011877$, $P > 0.05$; $R^2_{diameter} = 0.023889$, $P > 0.05$; $N = 144$). There is no relationship between fruit fate (hoarded and not hoarded) and fruit mass

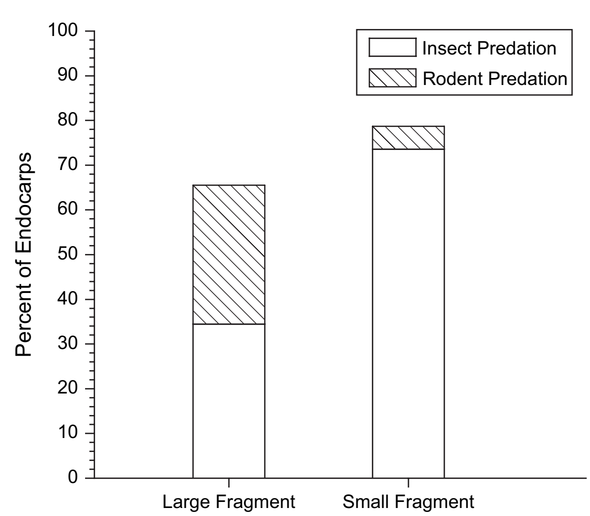

Fig. 4 – Percentage of *A. geraensis* endocarps preyed upon by insects and rodents in large and small Cerrado fragments in southeastern Brazil.

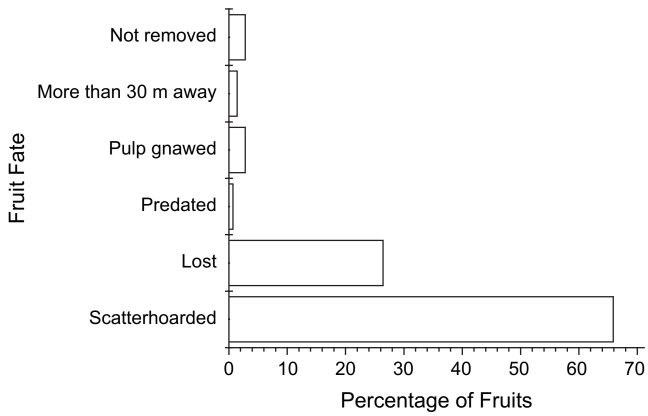

Fig. 5 – Fate of *A. geraensis* seeds in a large Cerrado fragment in southeastern Brazil.

(logistic regression, $\chi^2 = 0.99$, $P = 0.30$), length ($\chi^2 = 0.59$, $P = 0.44$) and diameter ($\chi^2 = 0.82$, $P = 0.36$).

4. Discussion

A. geraensis produces fruits throughout the year and its fruits have a hard mesocarp, characteristics which could satiate predators and increase the probability of dispersion by scatter-hoarding rodents. These characteristics are also found in others palms, such as *Attalea funifera* and *Attalea phalerata* (Reys, 2002; Voeks, 2002). The peak of fruit scarcity in the Cerrado occurs in July and August (Gottsberger and Silberbauer-Gottsberger, 1983), when most of the palms had fruits, with 75% of *A. geraensis* palms bearing fruits. This high frequency makes these fruits a reliable resource for frugivores in the Cerrado (Voeks, 2002). In fact, records of ripe fruits, considering the palms selected for the 12-month phenological study, occurred in the dry and in the rainy seasons (from May to December).

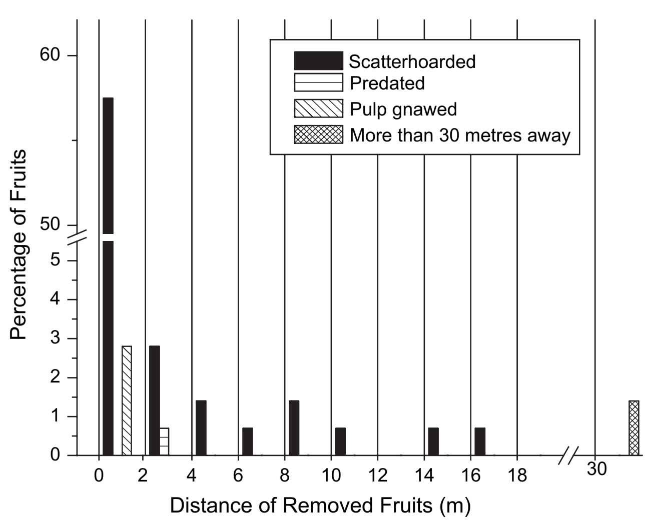

Fig. 6 – Fate of *A. geraensis* fruit in relation to the distance removed from the parent plant in a large Cerrado fragment in southeastern Brazil.

A. geraensis showed little variation in the number of fruits. Variation in seed number per fruit also occurs in two other palms of the same genus, *Attalea butyraceae* and *A. funifera* that have 1–3 seeds per fruit (Bradford and Smith, 1977; Voeks, 2002). Such variation in seed number may increase the probability of seed dispersal, even if some seeds are killed, especially by bruchids (Bradford and Smith, 1977). In the present study, however, all fruits classified as predated had all seeds killed.

In cases of fragmentation and defaunation, natural distributions of plants tend to be modified because of an increase in predation on non-dispersed seeds (Smythe, 1978; Wright, 2003; Galetti et al., 2006). Seed predation by insects was higher in the small fragment and could reflect the absence of agoutis in this area (Motta-Junior et al., 1996). The same pattern has been found for the palm *Astrocaryum aculeatissimum* in Atlantic rainforest fragments (Galetti et al., 2006).

Although both large and small fragments had a clumped distribution, the standardized Morisita's index was higher for the small fragment, indicating a more clumped pattern. Even though the distribution of reliable sites for recruitment was not recorded in the present work, the clumped pattern could reflect the loss of large scatter-hoarding species (agoutis) that usually disperse over larger distance (Donatti, 2004), while *C. bishopi* disperse seeds over short distances. Indeed, most palm species in the Cerrado show clumped distributions (Lima et al., 2003), especially those that depend on rodents for dispersal. *A. geraensis* is a fire-resistant species, and its distribution and dispersal characteristics are similar to those of *A. humilis* in Atlantic rainforest. The monospecific high-density stands in both species are the result of fire regimes and seed dispersal to favourable sites (Souza and Martins, 2002). The large size of *A. geraensis* fruits and lack of fleshy pulp make this species dependent on scatter-hoarding rodents, which are unlikely to move between distant fragments; this factor may be critical for the conservation of these palms (Souza and Martins, 2002). If our "lost fruits" and those dispersed >30 m away are considered as scatter-hoarded, the rate of scatter-hoarded fruits would increase to 93.7%. However, most fruits (57.5%) were scatter-hoarded at distances <2 m from the parent palms, which suggests a low gene flow through seeds, even within the large fragment.

The most likely current dispersers and predators of palm seeds are scatter-hoarding rodents, such as agoutis (Smythe, 1978, 1989; Forget et al., 1994; Wright et al., 2000) and spiny rats (Sánchez-Cordero and Martínez-Gallardo, 1998; Brewer and Webb, 2001; Wright et al., 2000). At our study sites, the phenological pattern of fruit production by *A. geraensis* could induce this seed predator to scatter-hoard some fruits (Vander Waal, 1990).

Since agoutis usually disperse seeds over larger distances than small rodents (Brewer, 2001; Brewer and Webb, 2001; Theimer, 2003; Donatti, 2004), they are probably the long-distance dispersal agents (more than 30 m from the parent plant), whereas *C. bishopi* disperses *A. geraensis* over a short distance. *A. geraensis* does not have fleshy pulp, and the hard nut can be dispersed only by two rodent species in the Brazilian Cerrado. The other *Attalea* species with fleshy pulp are also dispersed by tapirs, peccaries, and even raptors (Donatti et al., 2007; Galetti and Guimarães Jr., 2004). Hence, as predicted for large-seeded palms (see Galetti et al., 2006), *A. geraensis* has a very fragile dispersal system in the Cerrado, and we can predict that, in small Cerrado fragments, the absence of agoutis, which are the main long-distance seed dispersers of *A. geraensis*, can affect the gene flow via seeds and may produce a more clumped distribution of this palm. In highly disturbed Cerrado, where agoutis and spiny rats are extinct, *A. geraensis* is dispersed only by gravity and its genetic variability may be even more reduced.

5. Conclusion

Although some studies have examined the seed dispersal of *Attalea* palms in tropical forests, we are unaware of any work that has dealt with this matter in Cerrado populations. *A. geraensis* produces fruits throughout the year, which makes this species a reliable source of food for frugivores, especially specialized seed predator/dispersers. Only two rodent species (*C. bishopi* and *D. azarae*) scatter-hoarded the seeds and acted as *A. geraensis* seed dispersers. However, the dispersal distance was low and most fruits were scatter-hoarded less than 2 m from the parent plant, which may explain the clumped distribution seen in large and small fragments. In small Cerrado fragments, where the main *A. geraensis* dispersers are absent, dispersal distances may be even more reduced, thereby generating a more clumped pattern and higher insect predation.

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